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THE MARGARITIFERIDAE REINSTATED: A REPLY TO DAVIS AND FULLER (1981), "GENETIC RELATIONSHIPS AMONG RECENT UNIONACEA (BIVALVIA) OF NORTH AMERICA"

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ABSTRACT. Davis and Fuller (1981) proposed that the freshwater mussel family Margaritiferidae be reduced to subfamilial status, based on immunogenetic and morphological analyses of several North American unionoid species traditionally divided among the Unionidae and Margaritiferidae. They overlooked published studies contrary to their conclusions, provided little opportunity for alternative interpretations of their data, and failed to show the Margaritiferidae as a derived group within the Unionoida. It is proposed that the lineage which comprises all species exhibiting characters of the freshwater mussel genera *Margaritifera* and *Cumberlandia* may continue to be considered a distinct, derived family within the Unionoida.

Ortmann (1910) revised the freshwater mussel genus "*Margaritiana*" (now divided among *Margaritifera* and *Cumberlandia*) and in 1911 raised the genus to family level. He stressed the importance of certain anatomical characters unique to margaritiferids, including the absence of both a structurally formed diaphragm and vertical gill septa. He further argued that margaritiferids embodied the most

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primitive features among the unionoid mussels. Although challenged at first (Lefevre and Curtis, 1912), Ortmann's views soon found wide acceptance among unionoid systematists (see Heard and Guckert, 1970; Davis and Fuller, 1981; Boss, 1982, for review of classifications). Recently the familial status of the Margaritiferidae has again been challenged (Davis and Fuller, 1981). Although conceding the connotation of primitiveness and morphological distinctiveness of margaritiferids, they concluded that the group represents a subfamily of equal phylogenetic status with other traditional subfamilial groups in the Unionidae.

Davis and Fuller (1981) used information acquired from two sources: an analysis of immunogenetic data gathered from a wide assortment of taxa and a reassessment of the morphological characters of the "Unionacea."

Nonetheless, they neglected to leave open the possibility for alternative interpretation of their results and ignored extant studies relevant, though contradictory, to their own conclusions and further failed to explain why their concept of the Margaritiferinae demonstrates unique derived features distinct from other "unionid" groups. We present another viewpoint supporting the validity of the Margaritiferidae and to show that the Margaritiferidae represents a derived group within the Unionacea.

Davis and Fuller's (1981) immunogenetic analysis clearly showed three distinct clusters of taxa. Two clusters followed traditional systematic interpretations indicating a separation of an "amblemid" group from a margaritiferid group. A third cluster comprising the "anodontids" also was identified. They surmised that the anodontids represented as unique an assemblage as did the margaritiferids or amblemids. Furthermore, they determined that the 47% genetic distance they found between the margaritiferids and amblemids (no analysis was presented for margaritiferids versus anodontids or anodontids and amblemids combined) was insufficient to substantiate recognition of the Margaritiferidae. This conclusion followed a theory in which, among mollusks, genetic distance, expressed as ranges of percent differences between taxa, increased in a similar fashion with

morphological (*i.e.* traditional phylogenetic) distance. The criteria for family level status in "most" cases was from 50 to 80% (Davis, 1978). However, in a similar study involving immunogenetic comparisons of five unionid species, a sphaeracean clam, *Sphaerium striatinum*, and a marine veneracean clam, *Saxidomus nuttalli*, Fisher (1969) found that genetic distance did not increase in a similar fashion with "phylogenetic" distance. *Saxidomus nuttalli* and *Sphaerium striatinum* showed equal or less genetic deviation from certain unionids as did *Anodonta grandis*, a unionid species. Davis (1978) remarked that biochemical systematic studies on mollusks were just beginning so it may be premature to categorize higher molluscan groups according to genetic distance.

Nevertheless, in an electrophoretic study on five Palearctic species of Unionidae (genera *Unio* and *Anodonta*) and the margaritifera *M. margaritifera*, Logvinenko and Kodolova (1979) found that the level of similarity between the traditional unionid species and *M. margaritifera* was very low when compared to levels of similarity observed between each of the five unionid species. They concluded that the low level of similarity between the five unionid species and *M. margaritifera* was indicative of family level differences.

Davis and Fuller (1981) argued that morphological characters in "unionids" had undergone parallel evolution. Since parallel evolution prevented deviation from a basic unionid "groundplan" in margaritifera, they contended that margaritifera should not be accorded family rank. Unionoid bivalves (excluding etheriids) are infaunal filter feeders and show a morphological groundplan suited for such a role. In this respect most bivalve groups have undergone convergence or parallel evolution (Stanley, 1970). Davis and Fuller (1981) used certain marine bivalve families as examples to show the degree of difference between groundplans necessary for recognition of families. They consider the Cardiidae and Tridacnidae to have distinct enough groundplans to be considered as separate families within the Cardiacea. Similarly the Pectinidae, Malleidae, and Pteriidae (Pteriacea) are listed as showing family level groundplans. However, these families represent morphological adaptation

(groundplans) to vastly divergent niches and demonstrate such great morphological differences that some workers (Abbott, 1974; McCormick and Moore, 1969; Boss, 1982) consider most of them as distinct superfamilies (Tridacnidae in Tridacnacea, Cardiidae in Cardiaceae, Pectinidae in Pectinacea, and Pteriidae and Malleidae in Pteriacea). A more accurate comparison among recognized marine families should have included the Lucinidae and Mactromyidae (Lucinacea) in which an infaunal groundplan is present but in which other morphological differences substantiate recognition of separate families. The same is true for the Cardiidae and Hemidonacidae (Cardiaceae) and the Astartidae and Crassatellidae (Astartacea). The families above are distinguished by four or five major character states chiefly involving both the shell and anatomy (Boss, 1982).

In comparing margaritiferids with North American unionids Davis and Fuller (1981: Table 10, which see) listed morphological character states assignable to each taxonomic grouping. Characters one through four are of significant systematic importance as they represent substantive morphological differences in the adult morphologies of each group (see Boss, 1982, for accurate descriptions). Among the three subfamilies compared, the Anodontinae and Ambleminae share characters one through four, except that in character two a distinction is made between the Anodontinae and Ambleminae on the basis of the tripartite water tubes in the gills of the Anodontinae. The tripartite condition merely represents a specialization of the gill septa. Modifications of the female septate gill of lampsilines (within the Ambleminae of Davis and Fuller, 1981) occur as well. Modifications of the septate gill in both the Anodontinae and Ambleminae should therefore be included as part of the septate condition (character one). Characters five through nine can be considered of minor systematic importance because they are either highly variable among "unionid" genera or mutually inclusive (character five is inclusive with character two, and six with seven in the Ambleminae and Anodontinae).

Irregular teeth (ventral marginal teeth) on glochidial shells of margaritiferids (character six) are unique among unionaceans but are thus far known only in *M. margaritifera* (Harms, 1909; Smith, 1976) and possibly *M. laevis* (Okada and Ishikawa, 1959; Awakura, 1968). However, teeth are apparently absent in *C. monodonta* (Surber, 1915; Howard, 1915). "Variable glochidial shape" (character eight, Amblemninae) includes "subtriangular" (Anodontinae) and "subspherical" (Margaritiferidae). Determining the boundaries of "small," "medium," and "large" glochidia (character nine) is arbitrary and overlap exists.

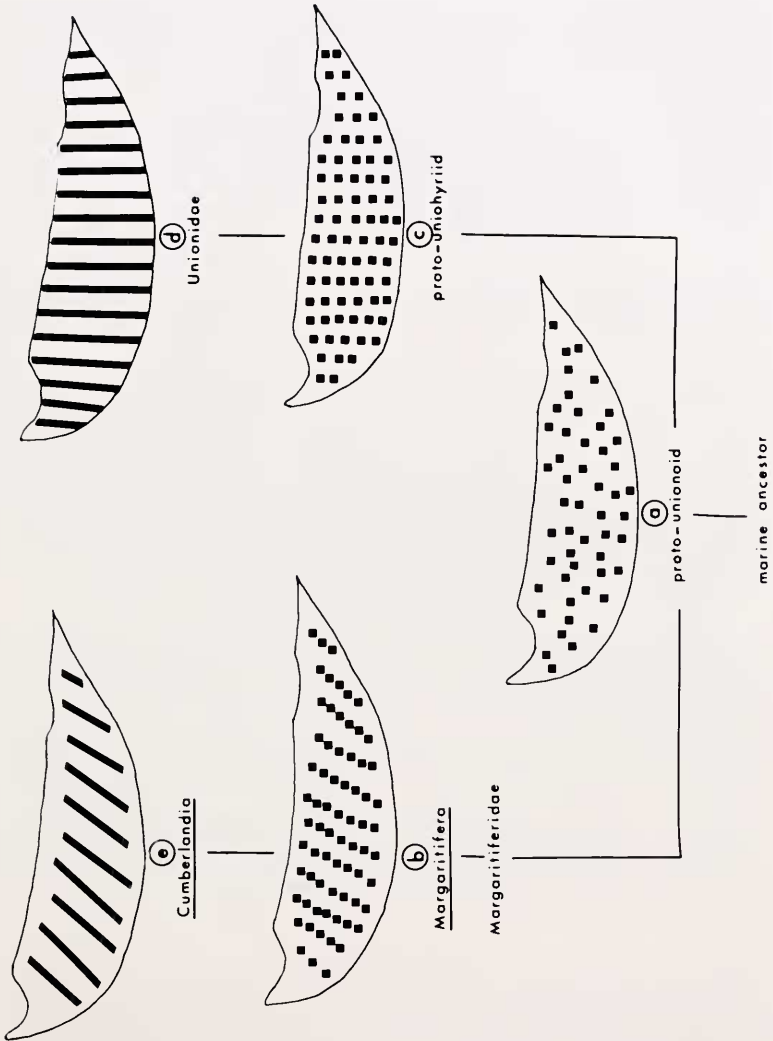
A conchological character separating the margaritiferids from the Nearctic and Palearctic unionaceans not discussed by Davis and Fuller (1981) concerns the presence of mantle-shell attachment scars on the inner surfaces of shell valves of margaritiferids (Pilsbry, 1896; Simpson, 1914). Smith (1983) discussed the histology and distribution of mantle-shell attachment in various species of the Margaritiferidae and mentioned the similarity between mantle-shell attachment scars in margaritiferid shells and scars in Recent trigonioid shells (Trigonioida). Newell and Boyd (1965) have rekindled historical arguments that propose a phylogenetic link between the marine trigoniids and unionoids.

Another overlooked conchological character distinguishing margaritiferids from unionids has been discussed by Tolstikova (1974) and involves the structure of conchiolin layers within the shell valves. She concluded that recognition of the Margaritiferidae and Unionidae as separate families was consistent with the degree of difference in shell structure between each group. Kat (1983) in a similar study has subsequently followed her conclusions.

Thus two conchological characters exist that separate margaritiferids from unionids; however, both characters are indicative of an ancestral condition (and therefore are not derived character states), the former (mantle-shell attachment) representing a carry over from a marine ancestor, and the latter from an unidentified freshwater ancestor which presumably gave rise to unionids as well (Kat, 1983).

The Margaritiferidae therefore differ from the anodontid-amblymid group by six character states (four anatomical, two conchological) which are equivalent to the number used to distinguish marine bivalve families with similar morphological groundplans. Had Davis and Fuller (1981) treated the Hyriidae they would have found that only three anatomical characters and no conchological characters (the morphology of conchiolin is unknown in hyriids) separate the Unionidae from the Hyriidae.

We believe that the margaritiferids diverged early from a stem unionoid group and followed a conservative evolutionary pathway independent of other unionoids. An ancestral eleutherorhabdic (=filibranch) group gave rise to freshwater inhabiting bivalves which acquired a synaptorhabdic (=eulamellibranch) gill condition in which solid interlamellar junctions replaced filamentous junctions to accommodate and brood shelled larvae. From a primitive eleutherorhabdic group a lineage evolved in which the randomly arranged interlamellar junctions (Text fig. 1a, the proto-unionoid stage) were arranged into diagonal rows (Text fig. 1b), a feature maintained in Recent margaritiferids. Another lineage evolved, the proto-uniohyriid, in which perforate (incomplete) vertical gill septa (Text fig. 1c), the alleged primitive state of septate unionoids (Heard, 1974), replaced randomly distributed interlamellar junctions. In later independent steps, perforate vertical septa became complete (Text fig. 1d). Both major branches aspired to accomplish a similar goal: to increase incubative efficiency. To this end the Margaritiferidae were largely unsuccessful as evidenced by the limited number of extant species and the lack of innovative marsupial morphologies otherwise present in unionoids. The culmination of marsupial design in margaritiferids exists in *C. monodonta* in which some of the scattered diagonally directed interlamellar junctions have coalesced to form diagonally elongated septa-like junctions (Text fig. 1e). A precursor to septa-like junctions (but not septa) is suggested by *M. margaritifera* in northeastern North America in which, during the incubative period, connective tissues are produced that line the inner gill lamellae walls and appear as diagonally arranged strands (Smith, 1979).



Text figure 1. Schematic diagram showing extant and assumed morphological states of the interlamellar junctions of gills of the Unionoida: a, the ancestral unionoid gill with randomized junctions (black squares); b, diagonally directed junctions in Recent *Margaritifera*; c, vertically directed junctions in proto-uniohyriids; d, vertical septa (fused junctions) in Recent unionids; e, fused diagonal junctions (non-septate) of Recent *Cumberlandia*.

A hypothetical freshwater ancestor common to both the Margaritiferidae and Unionidae and other unionoid groups, has been described herein containing a character state (randomized interlamellar junctions) not present in any living unionoid group nor found in any suggested hypothetical ancestral marine bivalve. Thus a character (anatomical) becomes available to identify the margaritiferids as a natural derived group within the Unionoida.

In summary, the moderate genetic distance between margaritiferids and unionids may not be fully interpreted at this time. However, the genetic distance exhibited by the margaritiferids represents the most discrete among "unionaceans" (excluding the Hyriidae, for which there are no genetic data). Furthermore, an alternative interpretation of morphological characters suggests that margaritiferids represent a distinct, derived group. Based on these arguments the Margaritiferidae is considered a valid family group.

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MISCELLANY

Dates of publication of the Molluscan portion (including the brachiopods) of the "Fauna del Regno di Napoli" (1829-1886) by Oronzio Gabriele Costa and Achille Costa.

by
Richard I. Johnson

This work was issued in signatures of varying amounts of text, at irregular intervals, and never completed. Sherborn (1910) pointed out that most of the signatures are dated and that the dates occur on, or near, the back fold of the signatures; thus they are mostly obliterated in bound copies of the work. Erasmo (1949) published the dates on the signatures based on a copy of the work in the department of zoology at the University of Bari, at the University of Naples, and on other copies elsewhere. He indicated the number of plates that appeared with each section but was unable to give their dates of publication. This is of little importance here, since nomenclature occurs on only one of the plates mentioned.

The unbound portion of the "Fauna" in my possession, and the bound one in the Museum of Comparative Zoology agree with the description given by Erasmo, except that he claimed the section on gastropods should have 19 plates, while both of these copies have only 18. The text for *Tritonium* mentions a plate 12, but it is not known if this was published, or if it is the plate referred to by Erasmo.

The author is very grateful to Dr. Robert Robertson of the Academy of Natural Sciences of Philadelphia for making a copy of Erasmo's work available from what may be the only set of the Journal, in which it appears, in the United States.